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Elevated temperature differently affects growth, photosynthetic capacity, nutrient absorption and leaf ultrastructure of *Abies faxoniana* and *Picea purpurea* under intra- and interspecific competition

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Head title: Warming affects plant-plant competition

Abstract The impact of global warming on plant-plant competition is yet to be fully understood. Resolving this knowledge gap is important for predicting the potential influence of global warming on forests, particularly on high-altitude trees, which are more sensitive to warming. In this study, we investigated intra- and interspecific competition in *Abies faxoniana* and *Picea purpurea* seedlings under control (ambient temperature) and elevated temperature (ET, 2 °C above ambient temperature) conditions for 2 years. We found that *A. faxoniana* and *P. purpurea* grown under intra- and interspecific competition showed significant differences in dry matter accumulation, photosynthetic capacity, nutrient absorption, non-structural carbohydrate (NSC) contents and leaf ultrastructure under ET conditions. ET significantly increased leaf, stem and root dry matter accumulation (DMA) of both conifers under both competition patterns. Moreover, under ET, *P. purpurea* possessed a better performance and had higher organ (leaf, stem and root) and total DMA, height growth rate, net photosynthetic rate, specific leaf area (SLA), water use efficiency ($\delta^{13}C$), leaf and root N and NSC contents, and more plasticity in N uptake forms compared to *A. faxoniana* under interspecific competition. Thus, the growth of *P. purpurea* benefitted from the presence of *A. faxoniana* under ET. Our results demonstrated that ET significantly affects competition patterns among conifer species in a subalpine region. It follows that global warming may alter plant-plant competition, thus influencing the composition, structure and functioning of subalpine coniferous forests.

Keywords: elevated temperature, plant-plant competition, conifer species, subalpine coniferous forests

Introduction

According to the IPCC report (IPCC 2013), the mean global surface temperature is forecasted to rise by 1.4 °C to 5.8 °C between 1990 and 2100, and the temperature increase will be most significant in high altitude and latitude ecosystems. Therefore, it is crucial to be able to predict how tree growth will respond to a warmer future environment, particularly in high-altitude regions. Many studies have demonstrated that warming can induce increased height and growth performance and biomass accumulation in tree seedlings, which are currently growing below their thermal optimum (Way and Oren 2010, Dieleman et al. 2012, Reich et al. 2018, Yuan et al. 2018). On the other hand, heat stress may reduce plant growth (Berry and Björkman 1980, Bauweraerts et al. 2014, Schippers et al. 2015).

Changed biomass allocation may be a way to improve plants' responses to climate change (Huang et al. 2015). For example, a meta-analysis conducted by Yuan et al. (2018) showed that warming has no effect on biomass allocation between roots and shoots, while Wertin et al. (2011) and Duan et al. (2018) reported that warming induces increased or decreased allocation to roots. In addition, warming normally increases total chlorophyll concentrations of trees (Wang et al. 2012, Zhao et al. 2012, Yuan et al. 2018). Similarly, warming can lead to increased leaf nitrogen (N) concentrations in conifers (Tingey et al. 2003, Luomala et al. 2005, Xu et al. 2012), and enhance nutrient cycling and increase nutrient availability (Rustad et al. 2001,

89 Melillo et al. 2011). Warming can also alter the storage of non-structural
90 carbohydrates (NSC, i.e. starch and soluble sugars), which act as a carbon buffer
91 when carbon assimilation cannot meet the demand (Sala et al. 2012, Pokhilko et al.
92 2014). In many species, elevated temperature has been found to reduce NSC
93 concentrations (Tingey et al. 2003, Way and Sage 2008, Duan et al. 2013).
94 Furthermore, tree seedlings are relatively sensitive to environmental stressors, and
95 they are typically exposed to competition with neighbors, rarely growing in isolation
96 in nature.
97
98 Plant-plant competition is a biotic factor that can affect plants' growth, species
99 abundance and distribution, and community composition (Michalet 2006, Raynaud et
100 al. 2008, Novoplansky 2009, Pierik et al. 2013). Adjustments in morphological and
101 physiological characteristics are fundamental ways for plants to cope with changes in
102 the resource availability and composition of neighboring plants, which, in turn, may
103 increase plants' competitive ability and fitness (Callaway et al. 2003, Anten et al.
104 2005). Abiotic factors, such as resource availability, often interact with plant-plant
105 competition (Niinemets 2010, Chen et al. 2014, 2015). Yu et al. (2017) have observed
106 that *Abies fabri* has a better performance and displays a higher net photosynthesis rate
107 and water use efficiency, and also a better N acquisition capability under interspecific
108 competition with *Picea brachytyla* when compared to intraspecific competition under
109 phosphorus fertilization. Duan et al. (2014) have discovered that under elevated
110 temperature, *Abies faxoniana* can change its nitrogen uptake and benefit from *Betula*

111 *albo-sinensis* under interspecific competition. Yet, there are still many uncertainties in
112 the mechanisms of morphological and physiological responses of plants (e.g.
113 subalpine conifers) to intra- and interspecific competition and warming climate.
114
115 Subalpine coniferous forests form the second greatest biome in China. *Abies*
116 *faxoniana* and *Picea purpurea* occur widely in these regions and contribute to the
117 maintenance of the ecological stability and succession of regional ecosystems (Wang
118 2004, Taylor et al. 2006). The most important limiting factors controlling the
119 performance of subalpine plants are generally considered to be a low temperature, low
120 nutrient availability and short growing season (Wang 2004, Hyvönen et al. 2007).
121 Previous studies investigating subalpine coniferous species have found that warming
122 shows a positive effect on plant growth and significantly increases photosynthesis and
123 biomass accumulation (Ran et al. 2013, Wang et al. 2013, Yin et al. 2013). For
124 example, a 6-year warming period significantly increased the leaf stem, root and total
125 biomass, specific leaf area and total chlorophyll concentration in *Abies faxoniana*
126 seedlings (Wang et al. 2012). However, previous studies have largely neglected the
127 interactions between plant-plant competition and warming, especially concerning
128 subalpine conifers, which are more sensitive to climate warming.
129
130 In the present study, we investigated the morphological and physiological responses
131 of *A. faxoniana* and *P. purpurea* to elevated temperature and intra- and interspecific
132 competition. Physiological and functional traits, such as growth traits, net

photosynthetic rate (P_n), chlorophyll fluorescence, leaf carbon isotope composition ($\delta^{13}C$), C, N and non-structural carbohydrate concentrations, and leaf ultrastructure were analyzed to discover the competitive ability of *A. faxoniana* and *P. purpurea* under elevated temperature and intra- and interspecific competition. Furthermore, different forms of ^{15}N-labeled ($^{15}NH_4NO_3$ and $NH_4{}^{15}NO_3$) were used to determine, whether there are differences in the N absorption of *A. faxoniana* and *P. purpurea* under elevated temperature and intra- and interspecific competition. The aim was to answer the following questions: (1) How does elevated temperature affect physiological and functional traits of *A. faxoniana* and *P. purpurea* under intra- and interspecific competition? (2) Do *A. faxoniana* and *P. purpurea* express different competitive strategies when exposed elevated temperature and interspecific competition? (3) Does elevated temperature change asymmetric competition outcomes in these two conifers?

Materials and methods

Study site, plant material and experimental design

This study was performed in the experimental area (2600 m above sea level) in the Wanglang National Nature Reserve (32°49'-33°02'N, 103°55'-104°10'E, altitude range 2,300-4,980 m), which is situated in the Pingwu County, western Sichuan Province, Southwest China. The details of climate, temperature and precipitation were described in Ran et al. (2013). In the Reserve, at elevations between 2800 and 3500 m, *A. faxoniana* and *P. purpurea* dominate on lower side slopes and alluvial bottomlands, whereas other *Abies* and *Picea*, *Betula* sp., and *Sabina saltuaria* grow on upper slope sites (Taylor et al. 2006). In addition, the life history of *P. purpurea* is characterized by longevity and high survivorship, which prevents the replacement by *A. faxoniana* (Wang 2004, Taylor et al. 2006). A total of 180 uniform-sized seedlings with a height of about 30 cm, 90 seedlings of *A. faxoniana* and 90 seedlings of *P. purpurea*, were selected from a nursery close to the station. At the end of September 2014, healthy *A. faxoniana* and *P. purpurea* seedlings were planted into plastic pots (two seedlings in each pot) with homogenized soil, which was obtained from the natural habitat of the two conifers. After adaptation to the environment for seven months, all seedlings were grown in growth chambers with a controlled environment from early May 2015 to the end of August 2016, and plants were harvested on 30 August 2016.

177

178 The chambers were almost cylindrical with 11 walls, the height of 3.45 m and the
179 internal ground size of 13.45 m^2. The chambers were made of hollow tempered glass
180 walls with a hollow polycarbonate top transmitting more than 85% of
181 photosynthetically active radiation (PAR). The natural photoperiod was 12 h
182 (0800-2000 h). The controlled environment was composed of air-conditioning,
183 automatic controlling, CO_2 injection mechanism and monitoring equipment for
184 environmental factors (e.g. total solar radiation, PAR, UV-B, and temperature). The
185 computer-controlled heating and cooling system, together with CO_2 sensors
186 (LT/WSK-PLC; Copeland and Vaisala, Beijing, China), can automatically adjust the
187 temperature and CO_2 concentration in the chambers to ensure a rise in temperature or
188 an ambient condition. The CO_2 level was kept at a similar level with the ambient
189 condition. Additionally, a water supply equipment with a monitor was used to control
190 air humidity.

191

192 The experimental design was randomized with three factors (species, competition and
193 temperature) and included two species (*A. faxoniana* and *P. purpurea*), two levels of
194 temperature (ambient temperature and 2 °C above ambient temperature) and three
195 competition setups, i.e., two intraspecific (*A. faxoniana* + *A. faxoniana* and *P.*
196 *purpurea* + *P. purpurea*) and one interspecific competition treatment (*A. faxoniana* + *P.*
197 *purpurea*). There were fifteen replicates per treatment. There were three control
198 chambers (ambient temperature) and three elevated temperature chambers (2 °C

above ambient temperature), each chamber including 15 pots (diameter of 36 cm, height of 40 cm). All pots were watered regularly to maintain non-limiting soil moisture throughout the experimental period. Furthermore, labeled $^{15}NH_4NO_3$ and $NH_4{}^{15}NO_3$ solutions were injected into the soil (5 cm depth) round the rhizosphere (30 mg/plant) in each treatment in the ^{15}N tracer experiment. Then, 72 h after the ^{15}N solution was applied, we harvested the plants and measured the ^{15}N values of leaves.

Determination of dry matter accumulation

We monitored the height and stem diameter of plants every week during the experimental period. The height and diameter growth rates (HGR, cm day^{-1}; DGR, mm day^{-1}) were calculated as (example for height) HGR = ($height_2$ – $height_1$) / (t_2 – t_1), in which the denominator is the period between the first and last measurements. Five seedlings were selected randomly from each treatment to determine the dry matter accumulation (DMA) at the end of the growth experiment. All harvested plants were separated into leaves, stems, coarse roots (>2 mm) and fine roots (<2 mm), then dried at the temperature of 70 °C for 72 h to, and the biomass was weighed. The root/shoot ratio (R/S) was determined as the ratio between total root DMA and aboveground DMA (the sum of leaf DMA and stem DMA). The leaf area was measured utilizing a scanner (Cannon Scanner 5600F, Chengdu, China) with 600 dpi resolution and imaging software (Image J; National Institutes of Health, Maryland, USA). The specific leaf area (SLA) was calculated as leaf area per dry mass.

221

222 *Determination of gas exchange and chlorophyll fluorescence*

223

224 The portable LI-COR 6400 photosynthesis measuring device (LI-COR, Lincoln, NE,
225 USA) was employed to measure the light-saturated net photosynthetic rate (P_n) in
226 healthy current-year leaves between 08:00 a.m. and 11:30 a.m. in the middle of
227 August 2016. We illuminated the target leaves with saturating irradiance (1000 μmol
228 m^{-2} s^{-1} PPFD) for about 5–20 min to gain complete photosynthetic induction before
229 starting the measurements. Conifer type chambers (PLC-broad, PP Systems) were
230 utilized under standard measurement conditions, as described by Song et al. (2017).
231 The mass-based photosynthetic N use efficiency (PNUE) was determined as the
232 mass-based photosynthetic rate (P_n) per the N content of leaves.

233

234 The portable fluorometer PAM-2100 (Walz, Effeltrich, Germany) was used to
235 determine the chlorophyll fluorescence of neighboring leaves in gas exchange
236 measurements according to the protocol of Schreiber et al. (1986). Additional details
237 were described in Chen et al. (2015).

238

239 Neighboring leaves used for P_n estimation were randomly sampled for chlorophyll
240 concentration determinations. The spectrophotometer UV-330 (Unicam, Cambridge,
241 UK) was employed to measure chlorophyll concentrations following the protocol of
242 Lichtenthaler (1987). The total chlorophyll concentration (*TChl*) was the sum of the

243 concentrations of chlorophyll *a* and *b*.

244

245 *Determination of C and N concentrations*

246

247 Plant samples (leaves, stems and roots) were collected from five randomly chosen
248 individuals from each treatment and ground into fine powder for C and N
249 determinations using the rapid dichromate oxidation method (Nelson and Sommers
250 1982) and the semi-micro Kjeldahl technique (Mitchell 1998), respectively.

251

252 *Determination of non-structural carbohydrates*

253

254 Plant samples (leaves, stems and roots) for non-structural carbohydrate analyses were
255 collected from five individuals chosen randomly from each experiment between 10:30
256 a.m. and 11:30 a.m. at the end of study (Chen et al. 2015). Around 50 mg of dry
257 powdered samples (leaves, stems and roots) were transferred into 10-ml centrifuge
258 tubes, followed by 30-min incubation in 80% (v/v) ethanol at 80 °C and centrifugation
259 at 5000 g for 10 min. The extraction was utilized for soluble sugar determination, and
260 the residue for starch determination. To prepare the residue for starch determination,
261 tubes with residue were left uncovered under the fume hood over the night to
262 evaporate the residual ethanol (Landhäusser et al. 2018). Glucose equivalents were
263 used to assay starch and soluble sugar concentrations by the anthrone-sulfuric acid
264 method (Yemm and Willis 1954). Methodological details were described in Chen et al.

(2015) and Song et al. (2017).

Determination of C and N isotope composition

DELTA V Advantage Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Inc., Waltham, Massachusetts, USA) was employed to measure the C and N isotope compositions. The same leaves used for P_n estimation were sampled for the C isotope composition ($\delta^{13}C$) determination. The C isotope content was shown as $\delta^{13}C$ values.

In the ^{15}N tracer experiment, $^{15}NH_4NO_3$ and $NH_4{}^{15}NO_3$ were used to reveal nitrogen uptake under different treatments, and the N isotope composition was expressed as $\delta^{15}N$. In each treatment, healthy leaves were sampled from the same upper position of the seedlings 72 h after the application of ^{15}N. Additional details concerning the C and N isotope analyses are given in Chen et al. (2014) and Song et al. (2017).

Transmission electron microscopy

Transmission electron microscopy (TEM) was performed using H-600IV TEM (Hitachi, Tokyo, Japan) for sections (2 mm in length) of healthy leaves neighboring those exposed to gas exchange measurements. The methodology followed Zhang et al. (2014).

Statistical analyses

Before performing statistical analyses, the data were examined for normality and the homogeneity of variances and, when needed, log-transformed to correct for deviations from the assumptions. Tukey's HSD tests along with one-way ANOVA were utilized to compare individual differences among means at the significance level $P < 0.05$. Differences between the temperature treatments were determined by independent-samples *t*-test. The effects of species, temperature and competition, and their interactions were determined by three-way ANOVAs. To gain deeper insight into intra- and interspecific competition, elevated temperature effects, and differences in physiological and functional traits, a principal component analysis (PCA) was conducted. Canoco 5.0 (Microcomputer Power, USA) was used for the PCA analysis. All data were analyzed with the Statistical Package for the Social Sciences (SPSS, Chicago, Illinois, USA), version 18.0.

Results

Effects of competition and elevated temperature on plant growth traits

Elevated temperature (ET) significantly increased leaf, stem, root and total dry matter accumulation (DMA) of both conifers under both competition patterns (Figure 1 a-e). Moreover, under ET condition, *P. purpurea* possessed higher organ (leaves, stems and roots) and total DMA than *A. faxoniana* under interspecific competition. Thus, the growth of *P. purpurea* benefitted from the interspecific competition under ET. In addition, the R/S ratio showed no significant difference among different treatments. The statistical analysis showed that the interaction of species × competition × temperature significantly affected stem, total root and total DMA, indicating that under ET, stem, total root and total DMA of *P. purpurea* had a greater increase under interspecific competition.

ET significantly increased HGR and DGR (height and diameter growth rate) of both conifers under both competition patterns (Figure 2). In addition, *P. purpurea* possessed higher HGR than *A. faxoniana* under ET and interspecific competition conditions. The statistical analysis showed that the interaction of species × competition × temperature significantly influenced HGR, indicating that under ET HGR of *P. purpurea* significantly increased under interspecific competition.

Effects of competition and elevated temperature on gas exchange and leaf ultrastructure

Under ET conditions, P_n, *TChl*, F_v/F_m and SLA of both conifers increased, and P_n, F_v/F_m, SLA and $\delta^{13}C$ of *P. purpurea* were significantly higher than those parameters in *A. faxoniana* under interspecific competition (Figure 3). In addition, ET had no effect of PNUE in either conifer species. The statistical analysis showed that the interaction of species × competition × temperature significantly affected *TChl* and SLA, indicating that under ET, *TChl* and SLA of *P. purpurea* increased more under interspecific competition.

The TEM observations of mesophyll cells showed that *A. faxoniana* and *P. purpurea* exhibited specific features under different competition and temperature treatments. Under control conditions, both conifers showed fewer chloroplasts and more starch accumulation. Under ET, *A. faxoniana* and *P. purpurea* exhibited smooth and continuous cell membranes and a typical chloroplast structure. Moreover, *P. purpurea* was characterized by bigger chloroplasts when compared to *A. faxoniana* under interspecific competition and ET conditions (Figure 4).

Effects of competition and elevated temperature on concentrations of C, N and non-structural carbohydrates

C concentrations of organs (leaves, stems and roots) changed slightly among different treatments, and ET significantly influenced the root C concentration. ET increased N concentrations but decreased C/N in all organs of both conifers. Moreover, *P. purpurea* showed a higher leaf N concentration than *A. faxoniana* under ET and interspecific competition conditions (Table 1). The statistical analysis showed that the interaction of species × competition × temperature significantly affected N concentrations of organs (leaves, stems and roots) and C/N ratios in stems and roots.

ET significantly decreased leaf starch and NSC concentrations of both conifers (Table 2). Under ET and interspecific competition conditions, *P. purpurea* possessed significantly higher concentrations of leaf and root starch and NSC than *A. faxoniana* (Table 2). The statistical analysis showed that the interactive effects of species × competition and competition × temperature significantly influenced NSC concentrations in organs, except for soluble sugars in stems.

Effects of competition and elevated temperature on $\delta^{15}NH_4^+$-N and $\delta^{15}NO_3^-$-N

Under interspecific competition and ET conditions, both conifers showed significantly higher $\delta^{15}NH_4^+$-N, and this was also significantly higher than $\delta^{15}NO_3^-$-N. Moreover, *P. purpurea* had the greatest $\delta^{15}NH_4^+$-N level under interspecific competition and ET (Figure 5). In addition, under ET treatment, interspecific competition decreased $\delta^{15}NO_3^-$-N of *A. faxoniana* more than intraspecific competition, while *P. purpurea*

expressed no differences between the competition patterns (Figure 5b).

Relationships among studied traits under different competition patterns and elevated temperature

The two components of the principal component analysis (PCA) explained 82.2% of the total variance of studied traits in *A. faxoniana* and *P. purpurea* in response to different competition patterns and temperature treatments (Figure 6). Control and elevated temperature experiments were separated along the second PCA axis. Under elevated temperature, the competition treatments of both conifers were clearly separated. Furthermore, *A. faxoniana* and *P. purpurea* were separated by the first PCA axis (Figure 6). PC1 was greatly affected by root starch, NSC and TS, leaf and stem TS, stem and root C and N, leaf C, stem N, HGR, DGR, PNUE, F_v/F_m and *TChl*. PC2 was strongly affected by leaf, stem, root and total DMA, SLA, P_n, leaf N, leaf and stem starch, NSC, and C/N. In addition, SLA and leaf N showed positive correlations with leaf, stem, root and total DMA and P_n.

Discussion

Competition and elevated temperature affect plant growth traits

Lavorel and Garnier (2002) and Fynn et al. (2005) have reported that growth and physiological traits can be used as indicators of plants' responses to competition and environmental factors. We found species-specific responses to elevated temperature (ET) and competition, particularly the interaction effects of ET and interspecific competition on the growth traits of *A. faxoniana* and *P. purpurea* were considerable. Under control conditions, there were no differences in stem, root and total dry matter accumulation (DMA) between intra- and interspecific competition in either conifer, while under ET conditions, leaf, stem, root and total DMA of *A. faxoniana* and *P. purpurea* significantly increased, as observed previously in conifers (Wang et al. 2012, 2013, Yin et al. 2013, Reich et al. 2018). Furthermore, *P. purpurea* possessed higher organ and total DMA than *A. faxoniana* under ET and interspecific competition (Figure 1 a-e). These findings indicated that under ET, the growth of *P. purpurea* benefited from the presence of *A. faxoniana*, whereas *A. faxoniana* seemed to be slightly inhibited under interspecific competition. This result was further supported by the significant interaction effect of species × competition × temperature on total DMA (Figure 1), which indicated that under ET, total DMA of *P. purpurea* increased more under interspecific competition. These interactive effects demonstrated that species-specific responses in DMA rise along environmental gradients (e.g.

419 temperature), but the results also indicated that the two conifers utilize different
420 growth strategies under climate warming.
421
422 Gedroc et al. (1996) and Lewis and Tanner (2000) have proposed that the
423 morphological and physiological plasticity of plants can change their allocation to
424 roots and shoots to cope with different environments. In this study, the R/S ratio of
425 neither conifer showed significant differences among different temperature treatments
426 (Figure 1f), which indicated that elevated temperature did not affect biomass
427 allocation between roots and shoots (as also in Yuan et al. 2018), or above- and
428 below-ground growth. In addition, *P. purpurea* possessed higher fine root and total
429 root DMA than *A. faxoniana* under ET and interspecific competition (Figure 1d). The
430 size of the root system plays an important role in the belowground competition (Lewis
431 and Tanner 2000, Rajaniemi 2002), as increased fine roots improve the capacity of
432 nutrient uptake and water and carbohydrate transportation (Fitter et al. 1998). The
433 relatively higher fine root and total root DMA of *P. purpurea* may play a key role in
434 contributing to the relatively higher N demand of continuously accelerated
435 photosynthesis under ET and interspecific competition. In addition, ET increased
436 HGR and DGR of both conifers (Figure 2), indicating that ET promotes tree height
437 and stem diameter growth (Xu et al. 2012, Wang et al. 2013, Fu et al. 2015), and
438 induces greater resource allocation to above-ground biomass, which also implies that
439 above-ground competition for resources (e.g. light) is important in trees (Suding et al.
440 2005) under global warming.

441

442 *Competition and elevated temperature affect photosynthetic capacity and*
443 *non-structural carbohydrates*

444

445 In the present study, ET significantly increased the net photosynthesis rate (P_n), total
446 chlorophyll ab (*Tchl*), F_v/F_m and SLA of both conifers (Figure 3), indicating that ET
447 had a positive influence on the photosynthetic capacity and growth (see also Xu et al.
448 2008, Fu et al. 2015, Huang et al. 2015, Reich et al. 2018, Yuan et al. 2018). This was
449 further supported by the mesophyll cell structure of leaves that showed that both
450 conifers exhibited smooth and continuous cell membranes and a typical chloroplast
451 structure under ET. This was ascribed to the more optimal temperature conditions for
452 gas exchange, as induced by warming (Wang et al. 1995). The photosynthetic N use
453 efficiency (PNUE) is an important functional trait of species closely related to their
454 leaf economics strategy (Hikosaka 2004). However, in the present study, ET showed
455 no effect on PNUE of *A. faxoniana* and *P. purpurea* (Figure 3d). This result is partly
456 similar to that of Duan et al. (2014), who found that ET decreased PNUE of *Betula*
457 *albosinensis* but had no effect on PNUE of *A. faxoniana*. In addition, previous studies
458 have showed that the N concentration of leaves is positively related to plants'
459 photosynthetic capacity across all biomes (Kattge et al. 2009, Xu et al. 2012), because
460 the N concentration of leaves is correlated with the Rubisco content (Field and
461 Mooney 1986). Our study showed that under interspecific competition and ET
462 treatment, *P. purpurea* possessed higher P_n, F_v/F_m and leaf N than *A. faxoniana*

463 (Figure 3ac, Table 1). The greater N acquisition capacity and lower long-term water
464 use efficiency (Figure 3f; Farquhar et al. 1989 and Livingston et al. 1999 have
465 discussed the interpretation of $\delta^{13}C$) could be highly important for the superior
466 photosynthetic performance of *P. purpurea* exposed to interspecific competition and
467 ET.
468
469 Reich et al. (1999) and Westoby et al. (2002) have demonstrated that plants with a
470 relatively high SLA are normally associated with high growth rates and a better
471 absorption of aboveground resources. In line with those studies, we found that *P.*
472 *purpurea* had a higher growth rate and SLA than *A. faxoniana* under interspecific
473 competition and ET (Figures 2a, 3e). The greater leaf area (leaf mass by SLA)
474 observed in *P. purpurea* demonstrates that a better capacity to enhance photosynthetic
475 productivity was the reason for its greater leaf, stem, root and total DMA relative to *A.*
476 *faxoniana* under interspecific competition and ET. There were positive correlations
477 among leaf, stem, root and total DMA, leaf N concentration, SLA and P_n according to
478 the PCA analysis (Figure 6). Moreover, under ET, the competition experiments of both
479 conifers were clearly separated from each other; *A. faxoniana* and *P. purpurea* were
480 separated by the first PCA axis (Figure 6). These results indicated that ET caused
481 species-specific responses under different competition treatments, as also supported
482 by the significant interaction effect of species × competition × temperature on many
483 studied parameters (total DMA, HGR, *TChl*, SLA, and N concentrations, etc).
484

Non-structural carbohydrates (NSC) can mobilize in plants, and their storage can serve as a buffer of energy in face of higher demands for growth or other physiological processes (Niinemets 2010, Wiley et al. 2013, Martínez-Vilalta et al. 2016). In this study, ET significantly decreased leaf starch and NSC concentrations of both conifers (Table 2), which is consistent with the observed leaf mesophyll structure: the presence of greater starch granules in both conifers under control conditions than under ET (Figure 4). This result matches previous studies, which showed that ET decreases the NSC concentration (Zha et al. 2001, Tingey et al. 2003, Zhao et al. 2012, Duan et al. 2013). One explanation for such decline in the NSC concentration is that ET increases the leaf respiration rate, which will lead to an increased consumption of assimilation compounds (e.g. soluble sugars and starch) (Tingey et al. 2003). In addition, *P. purpurea* exhibited higher concentrations of leaf and root starch and NSC when compared to *A. faxoniana* under interspecific competition and ET treatment (Table 2), indicating that *P. purpurea* has a better carbohydrate storage ability. The greater amounts of carbon storage reserves are important means for the responses of plants to environmental stress, such as drought and shading (Lawlor and Cornic 2002, Wiley et al. 2017). Furthermore, Kobe et al. (2010) and Pokhilko et al. (2014) have demonstrated that high root NSC may provide assimilation energy for nutrient absorption. Thus, the higher root N concentration might be due to the increase in the root NSC content of *P. purpurea* under ET and interspecific competition (Table 1), and the better ability of nutrient absorption might play an important role in the higher competitiveness of *P. purpurea* exposed to ET and interspecific competition.

507

508 *Competition and elevated temperature affect nutrient absorption*

509

510 In this study, ET did not increase leaf and stem C concentrations of either conifer
511 (Table 1), the reason possibly being the diluting effect of an increased growth. It has
512 been reported that leaf N concentrations of conifers increase under ET (Lewis et al.
513 2004, Luomala et al. 2005, Xu et al. 2012). As consistent with previous studies, we
514 found that ET significantly increased leaf N concentrations of both conifers (Table 1).
515 D'Orangeville et al. (2014) found that an elevated temperature increases the
516 mineralization of the forest floor and the N availability in soil, which consequently
517 leads to higher N concentrations in leaves (Bai et al. 2013). In this study, the C
518 concentration changed slightly and the N concentration increased significantly, thus
519 inducing a C/N decrease in all organs (leaves, stems and roots) of both conifers under
520 ET condition (Table 1). Opposite to our findings, Olszyk et al. (2003) and Wang et al.
521 (2012) claimed that warming increases the needle C/N ratio and decreases the needle
522 N concentration. In addition, under interspecific competition and ET, *P. purpurea* had
523 a significantly greater leaf N concentration than *A. faxoniana* (Table 1), indicating that
524 the former had a better capability to absorb N sources. Previous studies have
525 demonstrated that nutrient availability plays an important role in plants' competitive
526 ability and species composition (Portsmuth and Niinemets 2007, Boer et al. 2016).
527 For instance, N supply levels regulate carbon balance and affect the competitive
528 ability of *Larix*; *L. kaempferi* performs better than *L. olgensis* under N fertilization

529 (Guo et al. 2016). Evidently, a better ability for N absorption in *P. purpurea* can
530 enhance its competitive ability under interspecific competition and ET conditions.
531
532 ^{15}N isotope tracing was utilized to determine differences in N uptake forms between *A.*
533 *faxoniana* and *P. purpurea* under different competition patterns and temperature
534 treatments. We observed that under interspecific competition and ET, both conifers
535 had significantly higher $\delta^{15}NH_4^+$-N than in control treatments, and they showed
536 significantly higher $\delta^{15}NH_4^+$-N than $\delta^{15}NO_3^-$-N (Figure 5a, b). This result
537 demonstrated that under interspecific competition and ET, $\delta^{15}NH_4^+$-N is the main N
538 resource for *A. faxoniana* and *P. purpurea*. Moreover, under interspecific competition
539 and ET, *P. purpurea* had the highest $\delta^{15}NH_4^+$-N, which may be the key factor for its
540 higher leaf N concentration, and better growth performance and dry matter
541 accumulation. Earlier studies have reported that neighboring plants can influence the
542 absorption of different N forms (Miller et al. 2007, Ouyang et al. 2016). In this study
543 under ET, *A. faxoniana* had significantly lower $\delta^{15}NO_3^-$-N under interspecific
544 competition compared to intraspecific competition, while *P. purpurea* showed no
545 difference in $\delta^{15}NO_3^-$-N between the two competition patterns (Figure 5b). These
546 results indicated that *P. purpurea* has a greater plasticity concerning N uptake forms
547 under interspecific competition and ET treatment, as indicated by significantly higher
548 $\delta^{15}NH_4^+$-N and no changes in $\delta^{15}NO_3^-$-N, whereas *A. faxoniana* showed significantly
549 lower $\delta^{15}NH_4^+$-N and declining $\delta^{15}NO_3^-$-N under interspecific competition and ET.
550 Thus, the greater plasticity of N uptake forms in *P. purpurea* under interspecific

551 competition and ET condition will probably enhance its competitive ability and fitness
552 (see also Ashton et al. 2010, Duan et al. 2014).
553
554 Despite extensive research on plant-plant competition, little is known about the
555 interactions of warming climate and plant-plant competition on growth and
556 physiological traits in high-altitude plants. Duan et al. (2014) found that *Abies*
557 *faxoniana* was a superior competitor when compared to *Betula albo-sinensis* under
558 interspecific competition and warming conditions. In the present study, we showed
559 that intra- and interspecific competition and ET significantly influence dry matter
560 accumulation, nutrient absorption, photosynthetic capacity, non-structural
561 carbohydrates and leaf ultrastructure in *A. faxoniana* and *P. purpurea*, and ET alters
562 the competitive outcomes between the two conifers. Moreover, under interspecific
563 competition and ET condition, *P. purpurea* possesses a better growth performance and
564 competitive advantage. A better ability for resource storage (e.g., higher root N and
565 non-structural carbohydrates) and for the maintenance of carbon balance (e.g., higher
566 P_n, F_v/F_m and water use efficiency), as well as better plasticity concerning N uptake
567 forms make *P. purpurea* trees better competitors when grown with *A. faxoniana* under
568 ET.
569
570
571
572 **Conclusions**

The present study showed that elevated temperature (ET) can alter the competitive relationship between *A. faxoniana* and *P. purpurea*, thus influencing the composition, structure and functioning of subalpine coniferous forests. In nature, species generally interact with others and their surroundings. It is expected that *P. purpurea* first benefits from the presence of *A. faxoniana* and grows better under ET condition. However, invasive species are likely to be well adapted to global warming (Whutney and Gabler 2008). Furthermore, ET may have indirect effects on natural systems by affecting soil moisture (Brzostek et al. 2012) and the length of the growing season (Fu et al. 2014) as well as by altering plant phenology (Norby et al. 2003, Menzel et al. 2006). The complexity of natural systems constrains our capacity to predict the responses of plant-plant competition to ET in natural systems. Thus, a long-term field experiment is needed to investigate the natural systems under future global warming. Therefore, plant-plant competition should be considered in climate warming experiments and models predicting the potential responses of high-altitude plants to global climate warming.

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Conflict of interest The authors declare that they have no conflict of interest.

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Table 1. C and N concentrations and C/N ratios of leaves, stems and roots (mean ± SE) of *A. faxoniana* and *P.purpurea* under different competition and temperature (control versus +2 °C) treatments.

	Competition treatment	Leaf C (mg g^{-1})	Leaf N (mg g^{-1})	Leaf C/N	Stem C (mg g^{-1})	Stem N (mg g^{-1})	Stem C/N	Root C (mg g^{-1})	Root N (mg g^{-1})	Root C/N
Control	A/AA	506.36(1.70)a	10.57(0.24)c	47.99(1.08)a	472.54(1.49)a	6.61(0.03)b	71.50(0.53)a	413.20(3.08)a	8.34(0.03)a	49.54(0.46)a
	P/PP	498.70(2.01)bc	12.10(0.31)ab	41.33(1.14)bc	475.79(1.51)a	7.04(0.06)a	67.57(0.70)b	403.30(3.00)ab	8.34(0.11)a	48.40(0.83)a
	A/AP	504.59(1.24)ab	11.32(0.21)bc	44.61(0.81)ab	474.31(2.13)a	6.41(0.05)b	74.03(0.26)a	399.40(3.10)b	8.16(0.06)a	48.98(0.68)a
	P/AP	496.72(1.79)c	12.43 (0.19)a	40.01(0.72)c	476.09(1.57)a	6.49 (0.09)b	73.43(1.14)a	403.55(3.05)ab	8.35 (0.06)a	48.33(0.59)a
Elevated temperature	A/AA	$506.18(1.95)^{AB}$	$12.86(0.13)^{C***}$	$39.37(0.28)^{A***}$	$471.17(1.76)^{A}$	$7.58(0.15)^{A***}$	$62.26(1.29)^{A***}$	$409.39(3.29)^{A*}$	$9.15(0.05)^{A***}$	$44.77(0.56)^{B**}$
	P/PP	$498.90(2.09)^{B}$	$14.76(0.23)^{B***}$	$33.84(0.56)^{B***}$	$474.47(1.11)^{A}$	$7.19(0.07)^{A***}$	$66.03(0.59)^{A***}$	$410.05(1.89)^{A*}$	$8.86(0.03)^{B***}$	$46.29(0.25)^{B**}$
	A/AP	$508.14(2.33)^{B}$	$13.17(0.26)^{C***}$	$38.65(0.83)^{A***}$	$472.89(1.99)^{A}$	$7.21(0.13)^{A***}$	$65.65(0.93)^{A***}$	$410.17(2.57)^{A*}$	$8.22(0.04)^{C***}$	$49.93(0.39)^{A**}$
	P/AP	$500.09(1.62)^{B}$	$16.00(0.11)^{A***}$	$31.26(0.28)^{C***}$	$475.85(1.99)^{A}$	$7.51(0.10)^{A***}$	$63.36(0.84)^{A***}$	$411.02(1.41)^{A*}$	$8.81(0.13)^{B***}$	$46.68(0.68)^{B**}$
	$P:F_S$	0.000	0.000	0.000	0.028	0.109	0.214	0.590	0.019	0.041
	$P:F_C$	0.910	0.000	0.001	0.303	0.004	0.001	0.139	0.000	0.005
	$P:F_T$	0.198	0.000	0.000	0.388	0.000	0.000	0.010	0.000	0.000
	$P:F_{S\times C}$	0.855	0.410	0.941	0.699	0.195	0.265	0.076	0.000	0.014
	$P:F_{S\times T}$	0.970	0.002	0.465	0.789	0.026	0.017	0.357	0.572	0.971
	$P:F_{C\times T}$	0.201	0.450	0.534	0.822	0.009	0.003	0.058	0.000	0.001
	$P:F_{S\times C\times T}$	0.913	0.037	0.084	0.806	0.000	0.000	0.084	0.002	0.003

A/AA, *A. faxoniana* individuals from intraspecific competition; P/PP, *P. purpurea* individuals from intraspecific competition; A/AP, *A. faxoniana* individuals from interspecific competition; P/AP, *P. purpurea* individuals from interspecific competition.

Different lowercase letters indicate significant differences among the competition treatments within the control treatment and different uppercase letters within the elevated temperature treatment according to Tukey's tests ($P < 0.05$). The asterisks demonstrate statistically significant differences according to independent samples *t*-test between the temperature treatments within each competition treatment (* $0.01 < P < 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$.).

Three-way analyses of variance (ANOVA) were applied to evaluate the effects of different factors and their interactions. F_S, species effect; F_C, competition effect; F_T, temperature effect; $F_{S\times C}$, the interactive effect of species and competition treatment; $F_{S\times T}$, the interactive effect of species and temperature treatment; $F_{C\times T}$, the interactive effect of competition and temperature treatment; $F_{S\times C\times T}$, the interactive effect of species, competition and temperature treatment.

Table 2. Soluble sugar, starch and NSC concentrations of leaves, stems and roots (mean ± SE) of *A. faxoniana* and *P.purpurea* under different competition and temperature (control versus +2 °C) treatments.

	Competition treatment	Leaf soluble sugar (mg g^{-1})	Leaf starch (mg g^{-1})	Leaf NSC (mg g^{-1})	Stem soluble sugar (mg g^{-1})	Stem starch (mg g^{-1})	Stem NSC (mg g^{-1})	Root soluble sugar (mg g^{-1})	Root starch (mg g^{-1})	Root NSC (mg g^{-1})
Control	A/AA	75.23(2.25)c	114.19(3.89)b	189.42(4.69)b	31.65(0.77)a	83.81(1.41)c	115.45(2.13)c	30.29(1.06)b	47.38(1.69)b	77.67(1.70)b
	P/PP	104.09(2.51)a	72.21(3.89)c	176.30(2.52)c	35.38(1.41)a	100.06(3.84)b	135.44(4.62)b	12.47(0.39)c	12.89(0.43)c	25.36(0.40)c
	A/AP	90.54(0.53)b	108.36(2.83)b	198.90(2.75)b	34.16(1.84)a	111.11(2.05)a	145.26(1.46)ab	40.76(1.93)a	56.25(1.67)a	97.02(2.02)a
	P/AP	92.67(1.24)b	176.74 (2.78)a	269.42(2.19)a	31.71(0.71)a	120.33(1.10)a	152.04(1.49)a	26.10(1.02)b	51.64(1.38)ab	77.74(1.92)b
Elevated temperature	A/AA	$90.18(1.56)^{AB}$	$80.89(2.13)^{B**}$	$171.07(2.72)^{B**}$	$34.51(1.54)^{BC*}$	$85.05(1.53)^{BC}$	$119.56(2.46)^{C}$	$29.27(0.54)^{B}$	$38.58(1.02)^{C}$	$67.85(1.12)^{C}$
	P/PP	$94.79(1.43)^{A}$	$80.63(2.17)^{B**}$	$175.41(2.51)^{B**}$	$40.92(0.97)^{A*}$	$126.36(2.19)^{A}$	$167.28(2.55)^{A}$	$37.06(1.59)^{A}$	$55.72(1.63)^{B}$	$92.78(1.56)^{B}$
	A/AP	$82.44(3.15)^{B}$	$58.95(3.06)^{C**}$	$141.40(4.29)^{C**}$	$31.40(1.31)^{C*}$	$84.31(1.38)^{C}$	$115.71(1.05)^{C}$	$24.67(0.45)^{B}$	$30.32(0.75)^{C}$	$54.98(0.81)^{D}$
	P/AP	$90.64(2.07)^{AB}$	$120.54(3.82)^{A**}$	$211.19(4.07)^{A**}$	$38.65(0.96)^{AB*}$	$94.40(3.40)^{B}$	$133.05(3.03)^{B}$	$42.38(2.04)^{A}$	$72.82(4.61)^{A}$	$115.21(5.89)^{A}$
	$P:F_S$	0.000	0.000	0.000	0.000	0.000	0.000	0.064	0.001	0.064
	$P:F_C$	0.166	0.000	0.002	0.073	0.032	0.262	0.000	0.000	0.000
	$P:F_T$	0.433	0.000	0.000	0.001	0.001	0.094	0.000	0.000	0.000
	$P:F_{S\times C}$	0.000	0.000	0.000	0.140	0.000	0.000	0.001	0.000	0.000
	$P:F_{S\times T}$	0.003	0.000	0.086	0.001	0.000	0.000	0.000	0.000	0.000
	$P:F_{C\times T}$	0.009	0.000	0.000	0.240	0.000	0.000	0.000	0.000	0.000
	$P:F_{S\times C\times T}$	0.000	0.000	0.063	0.055	0.001	0.025	0.071	0.440	0.750

Treatment codes and statistical analyses as in Table 1.

Figure legends

Figure 1. Dry matter accumulation and partitioning of *Abies faxoniana* and *Picea purpurea* under different competition and temperature (control versus +2 °C) treatments. (a) leaf dry matter accumulation, (b) stem dry matter accumulation, (c) total root dry matter accumulation, (d) total dry matter accumulation, (e) fine root dry matter accumulation and (f) root to shoot (R/S) ratio. Each value is the mean ± SE (n = 5). Different lowercase letters indicate significant differences among the competition treatments within the control treatment and different uppercase letters within the elevated temperature treatment according to Tukey's tests ($P < 0.05$). The asterisks demonstrate statistically significant differences according to independent samples t-test between the temperature treatments within each competition treatment (***$P \leq 0.001$). Three-way analyses of variance (ANOVA) were applied to evaluate the effects of different factors and their interactions. S, species effect; C, competition effect; T, temperature effect; S × C, the interactive effect of species and competition treatment; S × T, the interactive effect of species and temperature treatment; C × T, the interactive effect of competition and temperature treatment; S × C × T, the interactive effect of species, competition and temperature treatment. A/AA, *A. faxoniana* individuals from intraspecific competition; P/PP, *P. purpurea* individuals from intraspecific competition; A/AP, *A. faxoniana* individuals from interspecific competition; P/AP, *P. purpurea* individuals from interspecific competition.

Figure 2. (a) Height growth rate (HGR) and (b) diameter growth rate (DGR) of *Abies faxoniana* and *Picea purpurea* grown under different competition and temperature (control versus +2 °C) treatments. Each value is the mean ± SE (n = 5). Treatment codes and statistical analyses as in Figure 1.

Figure 3. (a) Net photosynthetic rate (P_n), (b) total chlorophyll content, (c) the dark-adapted quantum yield of PSII (F_v/F_m), (d) photosynthetic nitrogen use efficiency (PNUE), (e) specific leaf area (SLA) and (f) carbon isotope composition ($\delta^{13}C$) of *Abies faxoniana* and *Picea purpurea* grown under different competition and temperature (control versus +2 °C) treatments. Each value is the mean ± SE (n = 5). Treatment codes and statistical analyses as in Figure 1.

Figure 4. Ultrastructure of mesophyll cells in *Abies faxoniana* and *Picea purpurea* grown under different competition and temperature (control versus +2 °C) treatments according to transmission electron microscopy (TEM). (a-d) control treatments: (a) A/AA, (b) P/PP, (c) A/AP, (d) P/AP. (e-h) elevated temperature treatments: (e) A/AA, (f) P/PP, (g) A/AP, (h) P/AP. The bar indicates 2 um (a). C, chloroplast; CW, cell wall; S, starch granule. Treatment codes as in Figure 1.

Figure 5. (a) $\delta^{15}NH_4^+$-N and (b) $\delta^{15}NO_3^-$-N of *Abies faxoniana* and *Picea purpurea* grown under different competition and temperature (control versus +2 °C) treatments. Each value is the mean ± SE (n = 5). Treatment codes and statistical analyses as in

Figure 1.

Figure 6. Principal component analysis (PCA) based on eco-physiological traits of *Abies faxoniana* and *Picea purpurea* under different competition and temperature (control versus +2 °C) treatments. The white circle, triangle, square and diamond indicate A/AA, P/PP, A/AP and P/AP under control conditions, respectively. The black circle, triangle, square and diamond indicate A/AA, P/PP, A/AP and P/AP under elevated temperature conditions, respectively. P_n, net photosynthetic rate; *TChl*, total chlorophyll content; F_v/F_m, the dark-adapted quantum yield of PSII; PNUE, photosynthetic nitrogen use efficiency; SLA, specific leaf area; Leaf TS, leaf total sugar concentration; Stem TS, stem total sugar concentration; Root TS, root total sugar concentration; HGR, height growth rate; DGR, diameter growth rate. Treatment codes as in Figure 1.

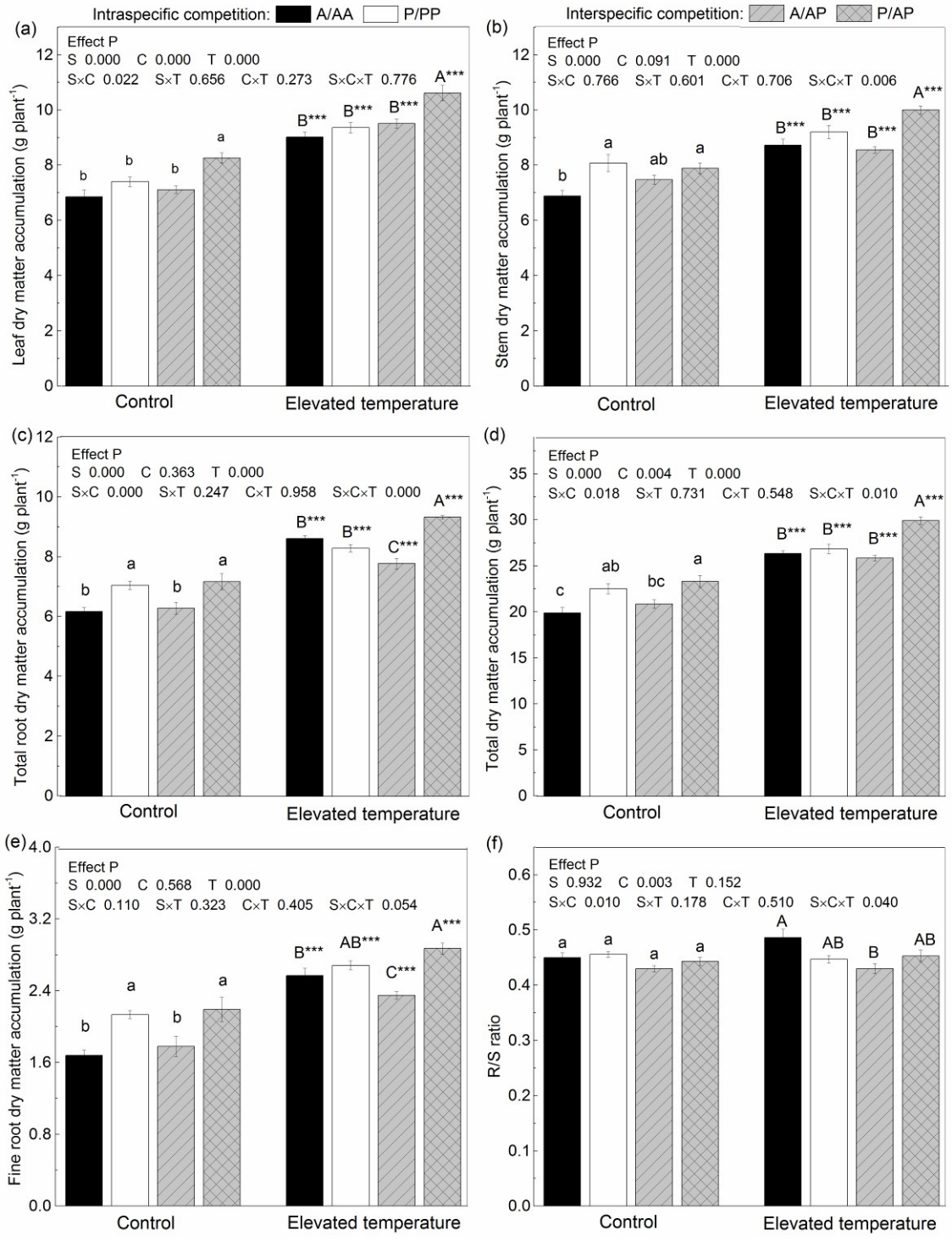
Intraspecific competition: A/AA P/PP
Interspecific competition: A/AP P/AP
(a)
Effect P
S 0.000 C 0.000 T 0.000
S×C 0.022 S×T 0.656 C×T 0.273 S×C×T 0.776
Leaf dry matter accumulation (g plant-1)
(b)
Effect P
S 0.000 C 0.091 T 0.000
S×C 0.766 S×T 0.601 C×T 0.706 S×C×T 0.006
Stem dry matter accumulation (g plant-1)
(c)
Effect P
S 0.000 C 0.363 T 0.000
S×C 0.000 S×T 0.247 C×T 0.958 S×C×T 0.000
Total root dry matter accumulation (g plant-1)
(d)
Effect P
S 0.000 C 0.004 T 0.000
S×C 0.018 S×T 0.731 C×T 0.548 S×C×T 0.010
Total dry matter accumulation (g plant-1)
(e)
Effect P
S 0.000 C 0.568 T 0.000
S×C 0.110 S×T 0.323 C×T 0.405 S×C×T 0.054
Fine root dry matter accumulation (g plant-1)
(f)
Effect P
S 0.932 C 0.003 T 0.152
S×C 0.010 S×T 0.178 C×T 0.510 S×C×T 0.040
R/S ratio
Control
Elevated temperature

Figure 1

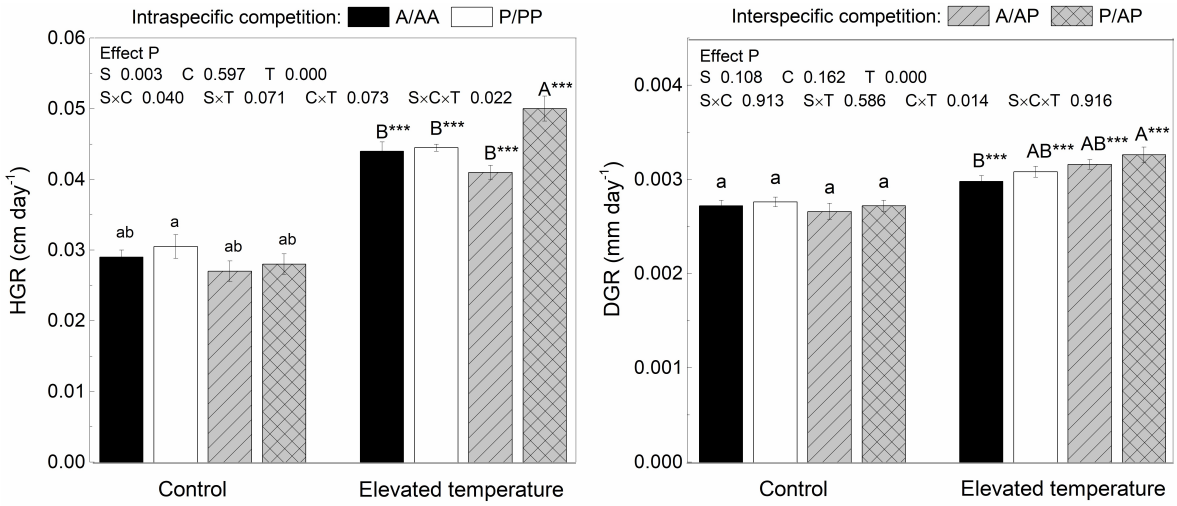
Intraspecific competition: A/AA P/PP
Effect P
S 0.003 C 0.597 T 0.000
S×C 0.040 S×T 0.071 C×T 0.073 S×C×T 0.022
HGR (cm day-1)
0.06
0.05
0.04
0.03
0.02
0.01
0.00
ab
a
ab
ab
B***
B***
B***
A***
Control
Elevated temperature
Interspecific competition: A/AP P/AP
Effect P
S 0.108 C 0.162 T 0.000
S×C 0.913 S×T 0.586 C×T 0.014 S×C×T 0.916
DGR (mm day-1)
0.004
0.003
0.002
0.001
0.000
a
a
a
a
B***
AB***
AB***
A***
Control
Elevated temperature

Figure 2

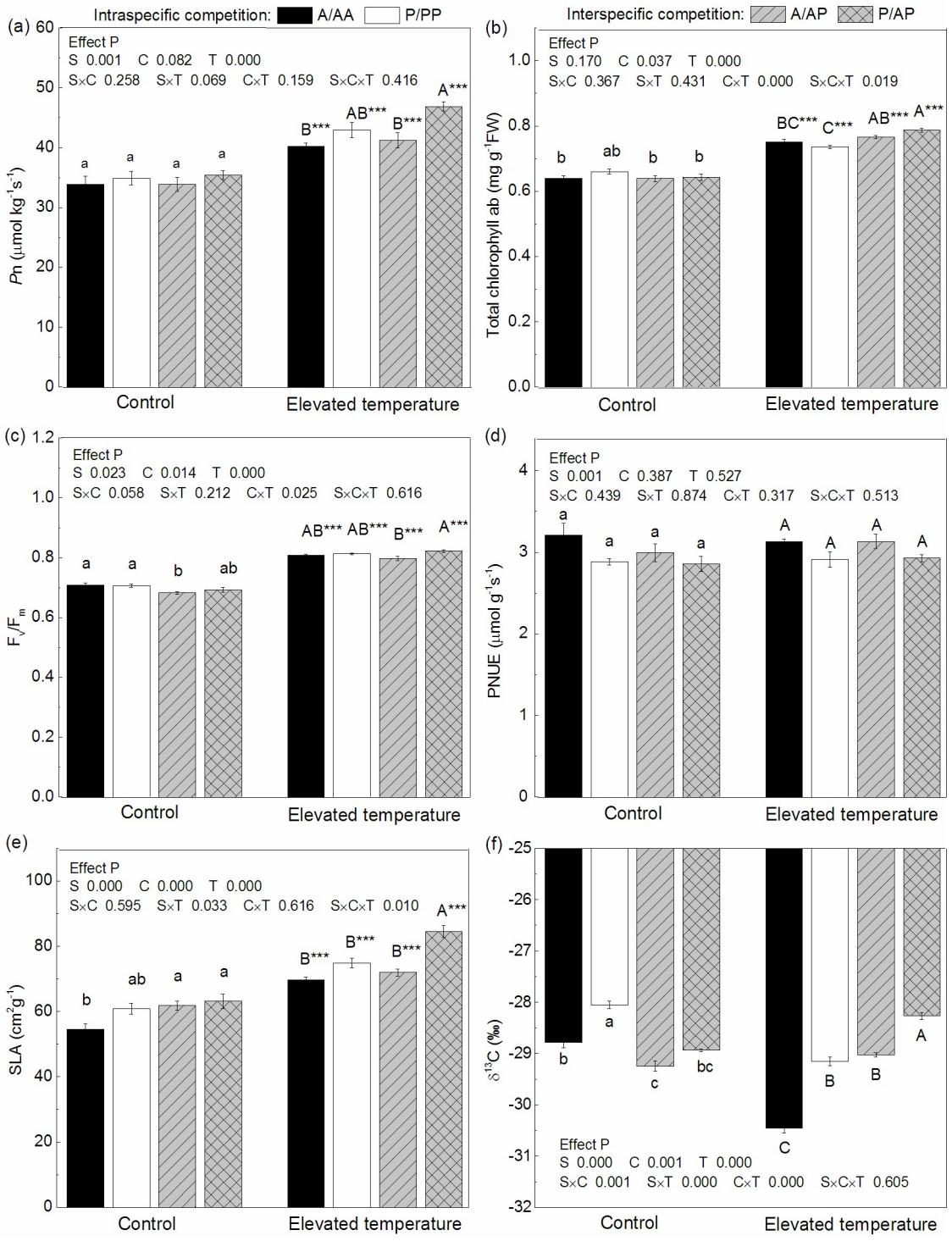
Intraspecific competition: A/AA P/PP
Interspecific competition: A/AP P/AP
(a)
Effect P
S 0.001 C 0.082 T 0.000
S×C 0.258 S×T 0.069 C×T 0.159 S×C×T 0.416
Pn (μmol kg-1s-1)
(b)
Effect P
S 0.170 C 0.037 T 0.000
S×C 0.367 S×T 0.431 C×T 0.000 S×C×T 0.019
Total chlorophyll ab (mg g-1FW)
(c)
Effect P
S 0.023 C 0.014 T 0.000
S×C 0.058 S×T 0.212 C×T 0.025 S×C×T 0.616
Fv/Fm
(d)
Effect P
S 0.001 C 0.387 T 0.527
S×C 0.439 S×T 0.874 C×T 0.317 S×C×T 0.513
PNUE (μmol g-1s-1)
(e)
Effect P
S 0.000 C 0.000 T 0.000
S×C 0.595 S×T 0.033 C×T 0.616 S×C×T 0.010
SLA (cm2g-1)
(f)
Effect P
S 0.000 C 0.001 T 0.000
S×C 0.001 S×T 0.000 C×T 0.000 S×C×T 0.605
δ13C (‰)
Control
Elevated temperature

Figure 3

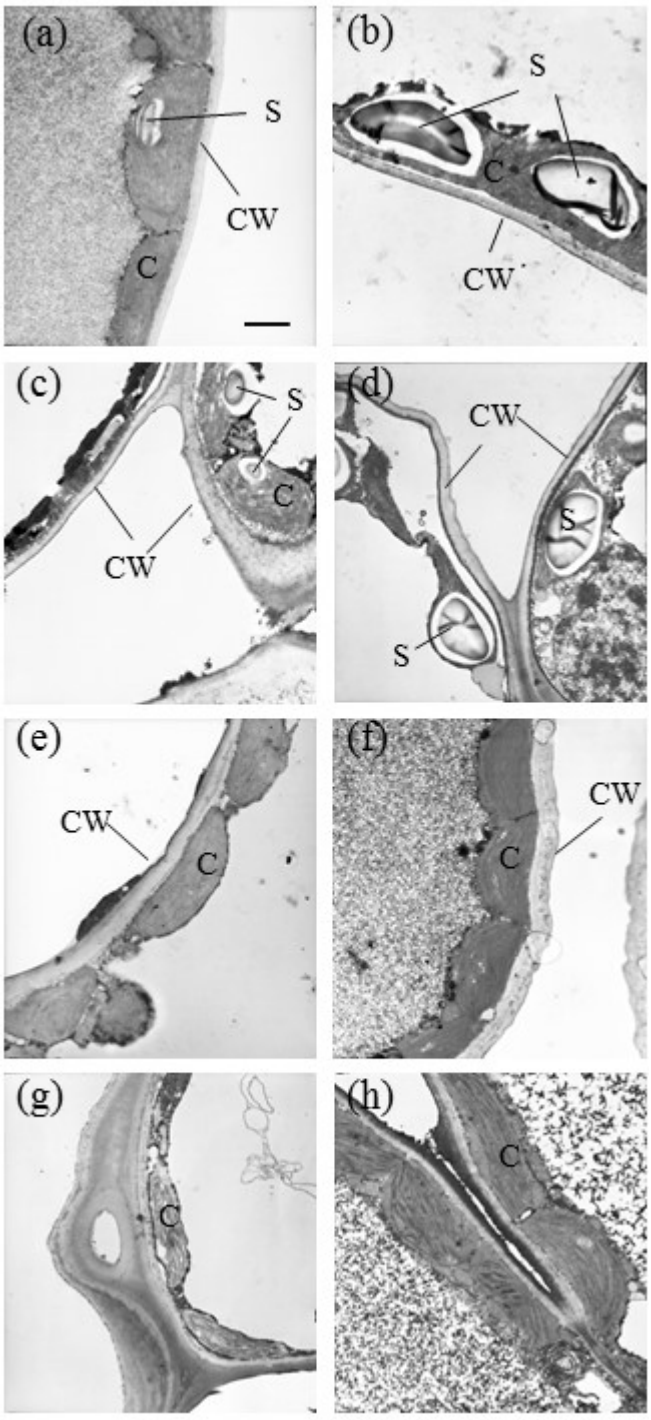

Figure 4

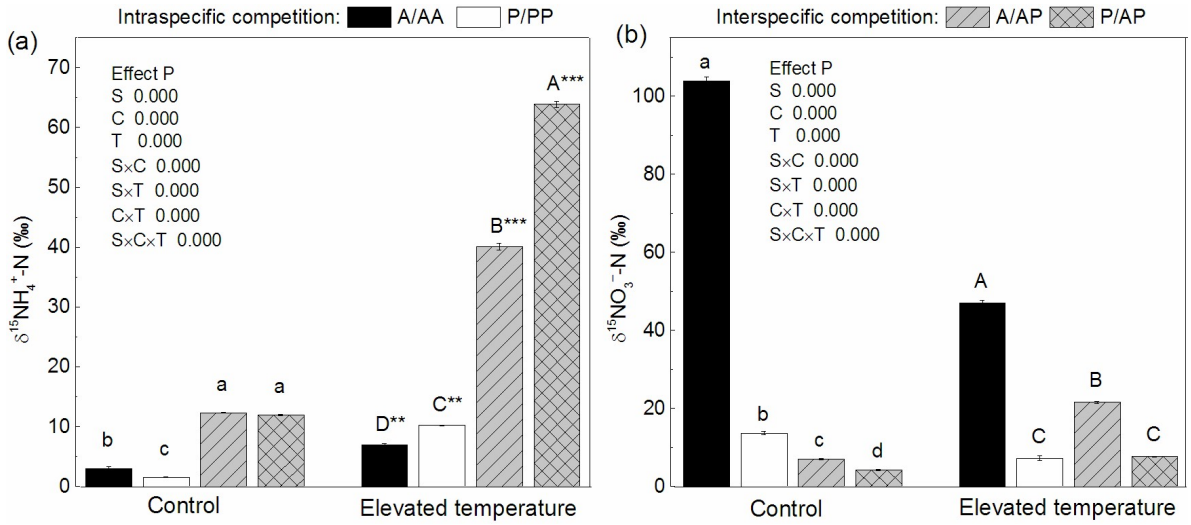
(a)
Intraspecific competition: A/AA P/PP
Effect P
S 0.000
C 0.000
T 0.000
S×C 0.000
S×T 0.000
C×T 0.000
S×C×T 0.000
δ15NH4+-N (‰)
b
c
a
a
D**
C**
B***
A***
Control
Elevated temperature
(b)
Interspecific competition: A/AP P/AP
Effect P
S 0.000
C 0.000
T 0.000
S×C 0.000
S×T 0.000
C×T 0.000
S×C×T 0.000
δ15NO3−-N (‰)
a
b
c
d
A
C
B
C
Control
Elevated temperature

Figure 5

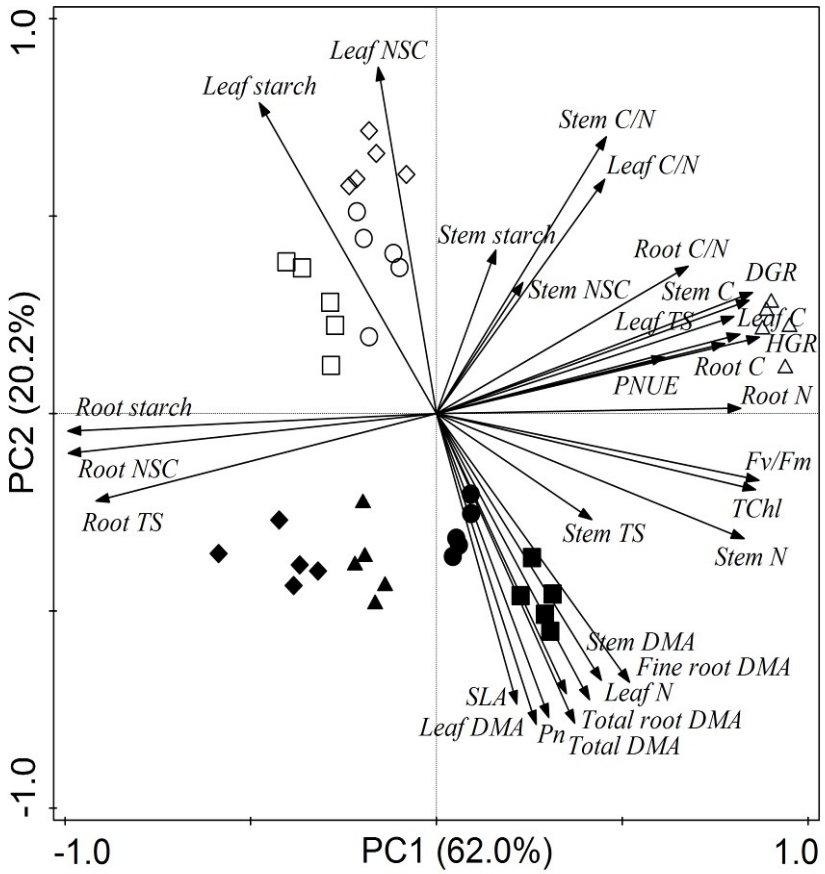
1.0
-1.0
PC2 (20.2%)
-1.0
PC1 (62.0%)
1.0
Leaf NSC
Leaf starch
Stem C/N
Leaf C/N
Stem starch
Root C/N
Stem NSC
Stem C
DGR
Leaf TS
Leaf C
HGR
Root C
PNUE
Root N
Root starch
Root NSC
Root TS
Fv/Fm
TChl
Stem TS
Stem N
Stem DMA
Fine root DMA
SLA
Leaf N
Leaf DMA
Pn
Total root DMA
Total DMA

Figure 6